

# THE EFFECTS OF A RECURRENT COASTAL PLUME ON THE DYNAMICS AND STRUCTURE OF THE LOWER FOOD WEB IN SOUTHERN LAKE MICHIGAN

Wayne S. Gardner and Peter J. Lavrentyev

## Abstract

The Lake Michigan Recurrent Coastal Plume (LMRCP) may fundamentally affect food web dynamics in Lake Michigan by causing major changes, during the winter-spring transition period, that, in turn, define the annual evolution of the biotic community in the lake. These effects can be observed by examining phytoplankton, zooplankton, and microbial food web structure and function in the field in combination with N-cycling studies that serve as an indicator of autotrophic and heterotrophic community dynamics. We hypothesize that: 1. The population growth of phytoplankton and bacteria are enhanced at the edge of the plume, where light levels are higher than inside the plume and nutrients are higher than in surrounding waters. The phytoplankton community structure will shift toward small-sized taxa in the plume relative to offshore waters. 2. The proportion of phytoplankton production consumed in the pelagic zone will, in turn, increase due to increase in herbivory by nano- and microzooplankton at the edge of the plume. 3. Increased growth and grazing rates of these consumers will lead to increased nutrient regeneration rates at the plume edge and increased high-quality food supply for crustacean zooplankton. To examine these hypotheses, we will compare structure and abundances of microbial food web organisms before, during, and after plume formation; measure N cycling rates in relation to community and species-specific grazing rates of microzooplankton within, at the edge, and outside of the LMRCP. Observations, experiments, and results will be coordinated with those from primary production and zooplankton grazing experiments and other studies of nutrient and physical processes to complete a conceptual model and provide data for the proposed coupled biological/physical model.

## Introduction :

An emerging paradigm in aquatic ecology is that some organisms are adapted to take advantage of a highly spatially and temporally varying environment (GLOBEC, 1992). Episodic events such as storms and turbidity fronts are recognized as important events in structuring planktonic communities (e.g. Mullin et al. 1985; Haury et al. 1992). Terrigenous and benthic input of nutrients and light-diminishing suspended solids influence growth and distributions of both primary and secondary producers (Boyton and Kemp 1985; Johengen et al. 1994). Phytoplankton and microzooplankton populations respond rapidly to both natural and anthropogenic perturbations (Nielsen and Kiørboe 1991; Lavrentyev 1994), because of their high growth rates, whereas population growth of crustacean zooplankton responds over longer time scales. Overall, the effects of large episodic events on the lower food web (here defined as a consortia of phytoplankton, bacteria, and nano- and microzooplankton) remain little known.

The fate of carbon fixed by phytoplankton is affected strongly by the composition of both the phytoplankton and grazers (Verity and Smetacek 1996). In oligotrophic temperate waters, such as southern Lake Michigan, large diatoms that are prevalent in the spring become replaced by smaller taxa as the summer progresses (Scavia and Fahnenstiel 1987). Although some copepods and protists, such as dinoflagellates, are capable of preying upon large and chain-forming phytoplankton (Hansen 1991; Vanderploeg 1994; Strom and Strom 1996), the large spring diatoms (e.g. *Melosira italica*) tend to settle quite rapidly out of the euphotic zone and are consumed by *Diporeia* and other benthic species (Gardner et al 1990; Quigley and Vanderploeg 1991). In contrast, small phytoplankton and associated bacterioplankton are readily consumed by microzooplankton that maintain the fixed energy (biomass) in the pelagic zone ( Sherr et al.1988).

As an inherent part of the herbivorous food web, microzooplankton (chiefly ciliates and dinoflagellates) use a significant proportion of pelagic primary production in temperate lakes in early spring (Muller 1989; Kustovliankina 1992; Gaedke and Striale 1994; Arndt and Mathes 1995; Sommaruga and Psenner 1995). Moreover, the growth rates of protists were correlated with and even

exceeded growth rates of phytoplankton during a spring bloom in a Danish lake (Hansen and Christoffersen, 1995). Although microzooplankton herbivory in the Great Lakes is not well understood, protists likely are important consumers of phytoplankton production because of their high abundances (Taylor and Heynen 1987; Carrick and Fahnenstiel 1989, 1990), turnover rates (Carrick et al. 1992; Lavrentyev et al. 1995), and grazing rates upon picoplankton (Fahnenstiel et al. 1991, Twiss et al. 1996). Importantly, microzooplankton are more efficient grazers of small (< 5  $\mu\text{m}$ ) phytoplankton than are crustacean zooplankton, especially large copepods (Fenchel 1986; Paffenhöfer 1984; Vanderploeg 1994; Dam et al. 1995).

Microzooplankton are, in turn, a preferable food source for planktonic crustaceans (Stoecker and Capuzzo 1990; Sanders et al. 1994; Atkinson 1996; Burns and Schallenberg 1996). Planktonic ciliates formed a substantial proportion of cyclopoid diets in Lake Constance (Gaedke and Straile 1994) and direct trophic links between microbial grazers and crustaceans have also been reported from Lake Michigan (Carrick et al. 1991). Adults of some copepod species have much higher clearance rates on ciliates than on algae (Burns and Gilbert 1993; Stoecker and Egloff 1987), with the proportion of ciliates in their diet increasing when small algae become predominant (Atkinson 1996, Brussaard et al. 1996; Lonsdale et al. 1996).

In both marine and freshwater systems, the microbial food web is of the utmost importance in supplying regenerated macro- and micronutrients for algal use in the pelagic zone (Caron and Goldman 1990; Haga et al. 1995; Selmer et al. 1993; Twiss et al. 1996). The trophic cascades involving protists can have profound effects on the efficiency of nitrogen remineralization (Miller et al. 1995; Suzuki et al. 1996) and autolithotrophic nitrification (Lavrentyev et al. in press). Although nitrogen does not normally limit phytoplankton growth in the spring in Lake Michigan, studying its dynamics provides valuable insights about community as well as organism dynamics (Haga et al. 1995; Miller et al. 1995). A critical nutrient for organisms, inorganic N is intrinsically involved in all biological processes in the pelagic zone. The dynamics of ammonium is of particular interest because it is the preferred form of N for phytoplankton and is usually the dominant form of nitrogen produced by heterotrophic mineralization of organic N (Campbell 1973). Measurements of ammonium uptake and regeneration, therefore, reflect the relative dynamics of autotrophic and heterotrophic processes and are critical to understanding intricate trophic interactions within the lower food web.

### **Implications of Large Episodic Events to Plankton Ecology in Lake Michigan:**

Preliminary examination of nutrient concentrations and organisms in water samples taken from within, at the edge, and outside (background station) of the Lake Michigan Recurrent Coastal Plume (LMRCP) in southern Lake Michigan in April 1996 indicate the spatial variability of abiotic and biotic parameters in the plume. "Available phosphorus" (i.e. labile P extracted with weak base solution) was higher at the mid-plume station than at the background station (Eadie et al. 1996). Diatoms predominated in the phytoplankton community in all three stations with more than 50% of their frustules accounted for by *Stephanodiscus* spp. However, there was a shift in their proportional biomass from the large oligotrophic *Rhizosolenia eriensis* and *Melosira italica* in the background station to the small (3-5  $\mu\text{m}$  in diameter) eutrophic *Stephanodiscus parvus* in the mid-plume (Table 1). Nanoplanktonic cryptophytes and picoplanktonic cyanobacteria, chiefly *Synechococcus* sp., as well as bacteria and nano- and microzooplankton were most abundant at the edge. The enhanced MFW activity at the edge of the plume, as indicated by the ratio of heterotrophic to photosynthetic carbon, may have resulted from phytoplankton production in this region, where elevated nutrient concentrations in the plume interacted with decreasing light attenuation.

The appearance of small diatoms is not unusual for the transition period in large temperate lakes. In Lake Baikal, the most abundant spring diatom, nanoplankton-sized *Stephanodiscus minutulus*, peaked at the edge of the thermal front (Likhoshway et al. 1996). Similar centric diatoms have been found to be a part of the spring flora in Lake Michigan (Holland 1969), especially in the waters near the eastern shore. On a lake scale, we know that the quantity and composition of phytoplankton strongly depend on available resources i.e. light and dissolved nutrients (Kilham and Hecky 1988, Makulla and Sommer 1993) that, in turn, is a major factor affecting the composition and production rates of organisms in the higher trophic levels, including fish (Rand et al. 1995).

**Table 1. The results of a pilot survey of the lower food web during the plume event in the southern Lake Michigan in April 1996 (T. Johengen and P. Lavrentyev - unpublished data).**

Parameter / Station	Background	Edge	Mid-plume
Chlorophyll a ( $\mu\text{g l}^{-1}$ )	1.81	1.83	1.55
Ratio of heterotrophic C to phyto C	0.43	0.70	0.22
Large diatoms (% of total phyto C)	62	28	20
Small diatoms (% of total phyto C)	22	41	60
Bacteria ( $\mu\text{g C l}^{-1}$ )	10.5	15.8	10.8
Picocyanobacteria ( $\mu\text{g C l}^{-1}$ )	5.3	11.6	5.9
Nanoflagellates ( $\mu\text{g C l}^{-1}$ )	2.4	4.5	2.6
Dinoflagellates ( $\mu\text{g C l}^{-1}$ )	1.0	2.9	0.3
Tintinnid ciliates ( $\mu\text{g C l}^{-1}$ )	4.4	5.6	5.0
Aloricate ciliates ( $\mu\text{g C l}^{-1}$ )	8.8	16.0	0.6

The LMRCP occurs during winter-spring, a crucial transition period for evolution of the annual biotic community. If the shift from large diatoms to smaller primary and secondary producers within the plume region generally holds for springtime plumes, the trend could fundamentally affect the fate of carbon fixed by diatoms and/or other phytoplankton, and may decrease the transport of diatom carbon to the benthos. The impacts of episodic events on phytoplankton and the microbial food web may cascade to upper trophic levels because the LMRCP occurs during the winter-spring transition, when the first generations of cyclopid and calanoid copepods (the dominant metazoan grazers in Lake Michigan) are produced by overwintering females and late copepodites (Torke 1975; Evans et al. 1980). The timing of the LMRCP may be also important. The 1996 plume occurred well before the onset of thermal stratification in Lake Michigan, so there was no interaction of plume dynamics with the development of the springtime thermal bar (Moll et al. 1993). However, in May 1981, a similar plume, also initiated by northerly winds, was apparent in satellite imagery well after thermal stratification had begun (Mortimer 1988). In this case, the plume material and developing thermal structure can interact to impact the springtime phytoplankton bloom and subsequent annual biological cycle.

### **Research Hypotheses and Objectives:**

Our primary hypothesis is that **large episodic events, such as the LMRCP, change the lower food web structure and increase its production in the pelagic zone.** The following specific hypotheses will be addressed:

- 1. The population growth of phytoplankton and bacteria is enhanced at the edge of the plume, where light levels are higher than inside the plume and nutrients are higher than in surrounding waters. The phytoplankton community structure shifts toward small-sized taxa in the plume relative to offshore waters.**
- 2. The dynamics of nano- and microzooplankton evolve differently inside and at the margins of the LMRCP than in the surrounding waters. The proportion of phytoplankton production consumed in the pelagic zone will increase at the edge of the plume due to increased herbivory by nano- and microzooplankton, and transport of phytoplankton carbon to the benthos will therefore be reduced.**
- 3. Increased growth and grazing rates of nano- and microzooplankton will lead to increased nutrient regeneration rates at the plume edge and increased food supplies for mesozooplankton.**

The study has three major objectives:

1. Compare population structure and species abundances of microbial food web organisms before, during, and after plume formation; 2. Measure N-cycling rates in relation to community and species-specific grazing rates of microzooplankton within, at the edge, and outside of the LMRCF; 3. Coordinate observations, experiments, and results from this study with the proposed studies of other biotic communities, nutrient dynamics, and sediment-trap collections as well as with the proposed coupled biological/physical model.

### **Research Plan and Methodologies:**

#### ***Lower food web composition and abundances:***

The aim of this survey sampling program is to determine the community structure and numerical distribution of the lower food web (here defined as phytoplankton and microbial food web organisms, including bacteria and nano- and microzooplankton) in relation to hydrodynamics of large-scale geophysical episodic events (Objective 1). This program will generate important biological information on the microplankton community response to the physical and chemical dynamics of the formation and dissipation of the LMRCF, and will help determine "key" species for experimental studies of community trophic interactions (Objective 2). It is important to consider taxonomic and functional structure of the planktonic community when applying the size-based models of trophic structure (Turner and Roff 1993; Strom and Strom 1996), because the intrinsic physiological rates and adaptations, morphology, feeding modes and mechanisms may vary within the same size category of plankton.

Samples will be collected from 3 transects in areas A, B, and C (see the cover document and [www.glerl.noaa/nsf-cop/lmplume.gif](http://www.glerl.noaa/nsf-cop/lmplume.gif) and [lm-phy.gif](http://www.glerl.noaa/nsf-cop/lm-phy.gif)) each consisting of 3 stations (mid-plume, the plume boundary and offshore of the plume). In the first year, sampling will be conducted during a two-week pilot cruise. In the years 2 and 3, we will take part in three cruises: before the plume is detectable by satellite imagery, during the evolution and lifetime of the plume, and after the plume dissipates. The sampling will be conducted in coordination with other research teams involved in this proposal (Objective 3). Specifically, we combine our efforts with Cotner et al., Fahnenstiel et al., and Bundy and Vanderploeg. At each station and sampling date, we will examine the following parameters: (1) abundance, biomass, and size structure of bacterioplankton as well as proportions of actively respiring cells (ARC); (2) abundance, biomass, and taxonomic composition of phytoplankton, including picoplanktonic cyanobacteria and eukaryotes; (3) abundance, biomass, and composition of nano- and micrograzers. Both protist and rotifer populations will be considered, with special attention given to mixotrophic ciliates and dinoflagellates. Sinking losses of diatoms will be determined from sediment trap chambers positioned near each station (Eadie et al. Proposal) to estimate export of diatom biomass to the benthos (Gardner et al. 1989, 1990; Scavia and Fahnenstiel 1987).

Total bacterioplankton will be counted from preparations stained with DAPI (Porter and Feig 1980) to reduce interference from detrital materials and clays in the plume. Size structure of bacterioplankton will be determined using fluorescent microspheres (Bratback 1993) and ARC will be determined using CTC-reaction (Rodriguez et al. 1995). Picoplankton-sized cyanobacteria and eukaryotes will be counted via epifluorescence microscopy from preparation made immediately after sampling, and stored frozen (Fahnenstiel et al 1991). Nanoplankton preserved with 1% cacodylate buffered glutaraldehyde (final concentration) will be counted using the dual-staining (FITC/DAPI) procedure (Sherr et al. 1993). Microplankton will be counted in settling chambers after fixation of whole water samples with 1% (final concentration) acid Lugol's iodine. Additionally, loricate ciliates, large dinoflagellates, colonial protists, and rotifers, that may not be present in sufficient numbers to be enumerated in the whole water, will be counted from samples pre-concentrated by gravity reverse filtration (Gifford 1991) using a 20- $\mu$ m net. Biomass of bacteria, phytoplankton, and microbial grazers will be estimated from their linear dimensions by approximating geometric solids and converting their biovolumes to carbon using the studies of Norland (1993), Montagnes et al. (1994), and Putt and Stoecker (1989), respectively. Taxonomic composition of protists will be determined from Protargol preparations (Montagnes and Lynn 1987; Skibbe 1994), and also qualitatively examined *in vivo* (Foissner 1991).

### ***Lower food web and nitrogen dynamics experimental studies:***

The purpose of this work is to examine the plume-induced changes on the partitioning of energy and nutrient fluxes through the pelagic lower food web. The experiments are designed to simultaneously measure growth, grazing, and metabolic rates of the nano- and microzooplankton as well as their species-specific feeding and growth rates in different parts of the plume. This part of the study will be conducted in Years 2 and 3 and tightly coordinated (Objective 3) with experiments on pigment-based growth and primary production of phytoplankton (Fahnenstiel et al. Proposal) and copepod grazing (Vanderploeg et al. Proposal).

We will use a novel combination of standard dilution experiments (Landry et al. 1995) and size-fractionation of plankton (Carrick et al. 1992) with fluorescently (Sherr and Sherr 1993) and  $^{15}\text{NH}_4^+$ -labeled prey (Suzuki et al. 1996). We will use a vital fluorescent stain CMFDA (Li et al. 1996) designed to overcome problems associated with heat-killed and surrogate prey (Landry 1994). Water will be collected during the LMRC event from the transects described above, gently screened through a 80- $\mu\text{m}$  mesh net to remove mesozooplankton, and placed in 1-l glass bottles. The samples will be gently diluted with the lake water sequentially prefiltered through 3.0- $\mu\text{m}$  and 0.2- $\mu\text{m}$  Gelman capsule filters, at the ratios of whole to filtered water of 0.5 to 0.2 in 0.1 increments. The bottles will be incubated at ambient temperature and light conditions in a rotating wheel (0.25 rpm). At the beginning and at the end of 24 h incubations, samples will be collected to determine plankton structure and biomass. The data from these experiments will be compared with pigment-HPLC measurements (Fahnenstiel et al. Proposal) to test the accuracy of dilution-based grazing rates (Waterhouse and Welschmeyer 1995). Growth rates of protists and their grazing mortality will be measured in the bottles with and without copepods of different life stages that will be added in known numbers (Vanderploeg et al. Proposal).

Community ammonium cycling rates will be used as a measure of trophic interactions (Legendre and Rassoulzadegan 1995; Suzuki et al. 1996). Ammonium uptake and regeneration rates will be studied in surface waters within, at the edge, and outside of the LMRC to examine the hypothesis that N-cycling rates are higher at the edge of the plume than in other regions. This hypothesis is supported by the fact that nutrient cycling rates are often enhanced in plume-edge regions where the availability of both light and nutrients are optimal for phytoplankton production and associated heterotrophic processes (e.g. Cotner and Gardner 1993; Gardner et al. In Press) and by our preliminary data indicating that abundances of protists were elevated at the edge of the LMRC (Table 1). This experiments will be coordinated with those on P uptake / recycling by the planktonic communities (Cotner et al. Proposal).

Ammonium uptake and regeneration rates will be estimated from isotope dilution experiments with added  $^{15}\text{NH}_4^+$  (Blackburn 1979; Caperon et al. 1979; Gardner et al. In Press). We will spike unfiltered samples with two concentrations (4  $\mu\text{M}$  and 0.5  $\mu\text{M}$ ) of  $^{15}\text{NH}_4^+$  and observe changes in ammonium concentrations and atom %  $^{15}\text{NH}_4^+$  enrichment over two time intervals to estimate "potential" and "near-actual" N cycling rates. Ammonium concentrations and atom %  $^{15}\text{NH}_4^+$  enrichment will be measured by direct injection high performance liquid chromatography (HPLC) (Gardner et al. 1993, 1995). In this unique cation-exchange technique, atom %  $^{15}\text{N}$  enrichment is determined directly in water filtrates by accurately quantifying the shift in ammonium retention time, caused by the presence of  $^{15}\text{NH}_4^+$  relative to an ammonium standard. The method requires only small samples (a few ml) and minimal sample-handling (filtering and freezing) because both concentrations and isotope ratios for ammonium are measured after directly injecting the thawed filtrates onto a high performance HPLC column. Assuming that organic substrate production by phytoplankton will be the factor controlling nitrogen cycling rates, we anticipate that nitrogen cycling rates in waters surrounding the edge of the plume and in the center of the plume will generally be near or below procedural detection limits (ca 0.03  $\mu\text{M h}^{-1}$ ) but that rates at the plume edge will be higher. Balanced experiments will be run under natural light (ca 50% attenuated) and in the dark, respectively, to gain further insights about autotrophic/heterotrophic interactions and to determine whether regeneration rates are enhanced under natural light as has been observed in the Mississippi river plume (Gardner et al. In Press).

To simultaneously measure microzooplankton herbivory and N cycling, small centric diatoms (*Stephanodiscus* sp.), previously grown in a culture with  $^{15}\text{NH}_4^+$  as the only source of N, will be additionally labeled by adding the fluorescent dye, CMFDA, to 1  $\mu\text{M}$  final concentration (Li et al. 1996), concentrated above a membrane filter, washed to remove excess  $^{15}\text{N}$  and the stain, and added into the triplicated experimental bottles containing 80- $\mu\text{m}$  screened lake water. The bottles will be enriched with natural-abundance  $\text{NH}_4^+$  to minimize  $^{15}\text{NH}_4^+$ -uptake and incubated at ambient temperature. The disappearance of labeled diatoms over time (1-3-6-12-24 h intervals) will be used as an internal measure of community grazing rates, whereas their accumulation in food vacuoles of protists over time (0.5-1-2 h intervals) will be used to estimate species-specific grazing rates. Accumulation of  $^{15}\text{NH}_4^+$  in the water sample over time will be considered to be the result of microzooplankton grazing on the labeled diatoms.

**Significance:**

The detailed information on lower food web structure, distribution, and trophic dynamics obtained in the proposed study will provide information on the ecological effects of large-scale episodic events in the Great Lakes. The responses of the microplankton community to episodic physical events may have important effects at the ecosystem level because these organisms play a pivotal role in nutrient transformations and in transfer of energy to higher trophic levels. Our species distribution and process study data will be synthesized with the results of other principal investigators in the larger LMRCF project, and particularly with the results from those studying the biotic effects of the plume. Because physical process in Lake Michigan are similar in many regards to those in the coastal ocean and because many microplankton organisms are ubiquitously distributed, our results and experience will also be useful for designing similar programs in other aquatic systems. These data also will be made available for incorporating into the proposed physical/biological model (Chen Proposal) to develop a more comprehensive understanding of both the physical causes and biological effects of the LMRCF in southern Lake Michigan and to enhance our ability to accurately predict the impacts of similar events in other large lakes and coastal ocean.

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